Payoff- and sex-biased social learning interact in a wild primate population

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SUMMARY

Social learning in animals is now well documented, yet few studies have determined the contexts shaping when social learning is deployed. Theoretical studies predict copying of conspecifics gaining higher payoffs [1-4], a bias demonstrated in primates only in captivity [5]. In the wild, research has shown selective attention towards the philopatric sex, a group's stable core [6]. Here we report the first rigorous experimental test of the existence of a payoff-bias in wild primates and its interaction with the sex of the model. We created a payoff bias in which an immigrant alpha male in each of three groups of wild vervet monkeys received five times more food upon opening a foraging box than did the philopatric alpha female, whereas in two control groups male and female models received the same amount of food. We tested whether this payoff asymmetry would override the previously documented selective learning from resident females. Group members were tested after having watched both models. When

both models received the same amount of food, audience members copied the female model significantly more than the male model, confirming previous findings. However, when a marked payoff bias was introduced, male, but not female, vervet monkeys significantly more often copied the male model receiving a higher payoff. These results demonstrate behavioral flexibility in the dispersing sex in these primates and suggest that the philopatric sex can afford to be more conservative in their social learning. Our findings show that multiple social-learning biases can coexist and interact within the same species.

RESULTS AND DISCUSSION

Numerous species, from insects, birds, and fish to cetaceans and primates, have been shown to acquire information or skills through social learning [7-15]. Social learning is the mechanism underlying cultural transmission and individuals can use different strategies to learn socially. Learning more about the evolution and underlying mechanisms of such cultural behavior in animals can help us better understand the evolution of humanity's distinctive cumulative culture [22]. Multiple hypotheses have been proposed to explain when and from whom individuals might be disposed to learn socially [1, 17-19]**.** The main distinction made is between direct (or content) biases, such as payoff-biased social learning, where attention is focused on characteristics of the observed behavior itself [17, 20, 21], and indirect (or context) biases, where individuals focus on particular individuals (for instance, they could copy high ranking or older individuals of their group) or commonly seen behavioral variants, without directly considering the payoff of the behavioral variants. Although theoretical models would suggest that selective attention to individuals yielding the highest payoff would be the most adaptive strategy, individuals have to be able to evaluate the value of a payoff and then to make a decision according to this evaluation. Because this may be too cognitively demanding, many species may have to settle for one or more of the indirect biases, such as copying what the majority of the group do or specific group members that could predict

success like older or high-ranking individuals. It is therefore important to test for the existence of a payoff-biased strategy in non-human primates. Moreover, humanity's success as a species depends on cumulative culture, and such a test could also allow us to better understand the evolution of cumulative culture, because a payoff-biased copying strategy could enable individuals to always adopt more beneficial behavioral variants, progressively enhancing their complexity.

Empirical studies in captivity have provided extensive support for context biases in social learning [17-20, 22, 23]. Field observations also confirmed that certain individuals, such as kin and older individuals are specifically looked to as 'models' for social learning [24-27]. Biases towards copying dominant individuals in social learning contexts have been found in some captive primates [22, 23] yet not in the only study to date in the wild [28]. Field experiments on vervet monkeys have revealed multiple social learning biases depending on the identity of the observers. Infants selectively copied their mother in both a food manipulation [25] and food choice [26] experiments. Immigrant males copied the local foraging norm in a food choice experiment despite possessing conflicting personal knowledge about what was the palatable and the unpalatable option [26]. Members of the philopatric sex (in the case of vervet monkeys, females) were more likely to be used as models in a two-action social learning task than members of the dispersing sex [6].

Some studies have reported payoff-biased social learning strategies in humans [2-4], captive chimpanzees [5], and fish [1]. Recently, Barrett and colleagues [29] described a form of payoff-biased strategy in wild white-faced capuchin monkeys. The researchers introduced a novel food item in a wild group of capuchins and observed the diffusion of extraction techniques that varied in their success rates, estimated as time needed to open the fruit. In our study, we expanded significantly on Barrett and colleagues by using multiple groups, including control groups, and a simple task in which similar actions could lead to variation of

rewards. Thus, we explicitly tested for the presence of a payoff-bias strategy and a potential interaction between social learning strategies, in a species of Old World monkey.

Testing the existence of payoff-biased strategies in a wild population of primates allows the discovery of whether they possess the cognitive abilities enabling them to make these adaptive choices, despite the diversity of information in their natural environment. Discovering whether such strategies operate in wild populations offers important progress in the study of cultural transmission. Mechanisms of social learning may be more deeply understood, by further identifying how individuals make decisions to learn socially.

In our experiment, we explored whether payoff-biased social learning operates in wild vervet monkeys and whether it may interact with, or override, the female-directed selective attention previously demonstrated in this species [6]. Vervet monkeys live in multi-male, multi-female groups. Females reside in their natal group for their entire life and form a linear dominance hierarchy with a stable matrilineal social structure [30]. Adult females and their offspring therefore form the core of the social group. Inbreeding is avoided through males dispersing into new groups when they reach sexual maturity (around 4-5 years old) and moving several times throughout their life (for more details see supplemental information).

An experimental contrast in which male models received greater payoffs than did females models (five pieces of apples vs one piece of apple) was created in three groups of wild vervet monkeys. In two other control groups, the two models received the same amount of food (one piece of apple). The artificial foraging box used during the demonstration phase had a door at each end with a separation in the middle (Figure 1), (see video S1 and S2 in supplemental information for more details). One side of the box was painted black and the other side white. The doors of the box were locked by an electric magnet that could be deactivated remotely by an experimenter when the desired social model was approaching.

Wherever possible, the highest ranking male and female in each group were trained as models (7 cases), but where this individual was unwilling to approach the box, we trained the individual immediately below it in the hierarchy (3 cases). Each model was trained to come to 'their' side of the box, either black or white, to extract a food reward (see Table S1 in supplemental information). Colors were counterbalanced across the different experimental groups. During the demonstration phase both models opened the box one hundred times to ensure that most group members had watched them. The experimental phase began directly after the demonstration. We offered boxes that looked the same but with both doors unlocked and lacked a separation in the middle, so every monkey could have access to both sides of the box (see video S3 in supplemental information for more details). Successful participants gained access to one single piece of apple placed in the middle of the box to avoid competition, this in both payoff-bias and control contexts. During this experimental phase we recorded which side monkeys approached and manipulated first, to see if they would choose first the female side or instead copy the model with the highest payoff, i.e. the male.

Vervets preferentially copy females so long as payoffs of males and females is similar

The first manipulation made by the monkeys is the most important one, as individual learning can influence subsequent choices. We therefore focused on the first choice made by group members in our analyses. We recorded a total of 65 individuals manipulating the box (Payoff-bias condition: 42 participants; Control condition: 23 participants), (see Table S1 in supplemental information).

As van de Waal and colleagues had reported for another population of wild vervet monkeys [6], we found that individuals preferentially copied the female model in the control condition, when female and male models received the same amount of food out of the box (proportion tests X^2= 5.261; n=23 p= 0.022; Figure 2A). However, in the condition where males obtained

greater rewards, there was no evidence that across all individuals, monkeys preferentially chose one side of the box first (male side or female side). Instead, they copied both sides equally (proportion tests X^2= 0.857; n=42; p= 0.355; Figure 2B). (See also supplemental results).

Biased attention does not explain the first choice made

One might expect the above result to be influenced by biases in visual attention. However, we found no correlation between the first choice individuals made and the side they had watched the most being opened during the demonstration phase by models, or was chosen during the experimental phase by any another individual, whether in payoff-bias or control conditions (One-tailed Spearman correlation: Payoff-bias: r= -0.091; n=42; p= 0.566; Control: r= 0.026; n=23; p=0.907, N=23). Thus, we found no evidence that individuals chose to preferentially copy the female or male model depending on how often they had attended to one model or the other. These results suggest that either the model's identity or the quantity of food extracted from the box was more important for the monkeys' decision-making than the amount of experience they had gathered of a specific side being open during the demonstration phase. (See also supplemental results).

Sex of observer monkeys also influenced their first choice

Using Generalized Linear Models (GLM), we controlled for the influence of several participant characteristics, namely sex, age, rank, group identity, and kinship (degree of relatedness) with the female model and with the male model. Results showed that in the payoff-bias condition where the male model received a greater reward than the female model, males tended to copy the male model more, whereas females copied the female model more (GLM, n=42, p=0.005; Figure 3A & Table 1). However, this effect did not occur when female and male models obtained the same amount of food (GLM n=23, p=0.683; Figure 3B & Table

1). Indeed, when analyzing the choice made by male participants only, we found significantly more males copying male models in the payoff-bias condition than in the control condition (proportion test X^2= 6.250; n=16, p= 0.012). By contrast we found no difference in the number of males copying the female side depending on the experimental condition (proportion test X^2= 0.059; n=17, p= 0.808). Turning to the choice made by female participants, we found that the experimental conditions had no influence on the choice of the females (proportion test, when females copied the female models: X^2= 2.130; n=23, p= 0.144; when females copied the male models: X^2= 0.500; n=8, p= 0.480). We found no significant influences of the other factors included in our model (age, rank, group, kinship with female model, and kinship with male model) for either the experimental condition or the control condition (Table 1).

Our most striking and novel finding is that if potential male models are seen to gain greater payoffs than resident females, who are normally the preferred models for social learning, male vervet monkeys copy the more successful male model significantly more often than in the control condition, whereas female monkeys persist in copying the female model despite her lower success. That a payoff bias can override the normal selective attention of male vervet monkeys toward female models suggests greater flexibility in the social learning rules of the dispersing sex in this species. More generally this implies that a monkey is capable of using multiple social learning strategies in combination, contingent on the conditions that the individual is exposed to.

Our results thus reveal an interaction between as many as three variables influencing vervet monkey decisions about social learning: pay-offs obtained by potential models, the sex of the model, and the sex of the observer. Such complex contingencies may be explicable by the behavioral ecology of vervet monkeys. First, as the males are the dispersing sex in this

171 species, they might benefit from greater behavioral flexibility than females because they have
172 to integrate into a totally new group when they migrate. Such dispersal is a very difficult
173 period marked by a number of potentially risky situations. Upon leaving the safety of their
174 natal group, males must quickly find a new group to join, as a lone monkey is more
175 vulnerable to predators. Then on immigration, males are often threatened and injured by the
176 individuals (males or females) from the new group [31]. They typically begin life in their new
177 group as low rankers [31, 32]. Thus, to integrate into a new group, being able to behave
178 flexibly may be adaptive, especially with regard to social learning rules. Such flexibility
179 would enable integrating individuals to adopt the most efficient strategy to learn from others
180 depending on the situation, and by copying the most successful individual, they may adopt the
181 most beneficial behaviors. Learning socially the habits of the males when gaining a higher
182 reward might also increase the survival and fitness of integrating males by copying their rivals
183 when successful. Accordingly, we would predict that in species where females are the
184 dispersing sex, as in chimpanzees [33], the sex effect would be reversed.

185 A previous study on the same vervet monkey population revealed that after dispersing, males
186 were prepared to flexibly abandon their own earlier, experimentally induced preference for
187 one of two alternative colors of provisioned corn for the one preferred by their new group
188 [26]. Thus, dispersing males appear to respond more to their social knowledge than their
189 earlier personal experience concerning food choice. The results of this study indicated a
190 disposition for conformity in the males, in that they abandoned their habitual preferences in
191 favor of those of a majority of others feeding in their new group [26]. Critics have argued that
192 assuming conformity may be premature, because immigrant males might be using other rules
193 such as copying the most high-ranking individual in the group [34]. However, this latter
194 explanation has recently been tested, with negative results [28]. The present results provide

195 support for the presence of bases of social learning that may complement conformist biases in
196 dispersing males and provide adaptive forms of behavioral flexibility.

197 Female vervet monkeys did not exhibit the same behavioral flexibility as males. For females,
198 in a species where they are the philopatric sex, it may be more adaptive for them to behave
199 relatively conservatively, maintaining close and strong bonds with the other philopatric
200 females in their group, and to be less disposed to copy immigrants unlikely to have an
201 efficient local feeding behavior. A positive influence of bonding on females' fitness and their
202 infants' survival has been well documented in baboons, in which females are also philopatric
203 [35, 36]. Indeed, female philopatry is common in Old-World monkeys and our findings may
204 be found to generalize to many other such species [37, 38]. In vervet monkeys, the only
205 reported case of females leaving their natal group was when a group became too large for the
206 available resources and a sub-unit of low-ranking females fissioned from the main group,
207 starting a small splinter group [39]. A study employing the same colored corn tests revealed
208 that splinter females showed a 100% fidelity to the color preferred by their origin group,
209 despite being in a new social unit, and in a new home range, and prior experience that both
210 colors were now palatable [39]. This emphasizes the constancy and conservatism of behavior
211 in female vervet monkeys; our current findings are highly consistent with this.

212 Our results emphasize the flexible social learning strategies of the dispersing sex in this
213 species of primate, whereas the philopatric sex appears to be more conservative. More
214 generally, our study reveals that multiple social-learning biases may interact within the same
215 species depending upon characteristics of the learner and the conditions to which they are
216 exposed. Sex differences in social learning have also begun to be reported in both human
217 children [40, 41] and adults [42]. The interplay between multiple social learning rules has
218 begun to be investigated in developmental psychology [43, 44]. However, our experimental
219 study is explicitly testing for, and highlighting, such complexities in non-human primate

behavior, and it does so in the wild, where primates are embedded in a multitude of complex decisions about such factors as foraging, predator avoidance, mating and social relationships from moment to moment. We may only now be beginning to appreciate not only the pervasiveness of social learning among animals [11, 45], but also some of the complexities of their adaptive social learning biases.

SUPPLEMENTAL INFORMATION

Supplemental information includes five tables, and three videos of the experiment.

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AUTHOR CONTRIBUTIONS

E.W., A.W. and C.S. designed the experiment. A.B. conducted the experiments, ran the statistical analyses and wrote the first draft. E.W., A.W. and C.S wrote the second draft. E.W. was granted the funding for data collection. F.E. and A.S. ran the genetic analyses. M.K. supervised the genetic analyses and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Laland, K.N. (2004). Social learning strategies. Anim. Learn. & Behav. 32(1), 4-14.

2. McElreath, R., Lubell, M., Richerson, P.J., Waring, T.M., Baum, W., Edsten, E., Efferson, C., and Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. Evol. Hum. Behav. 26(6), 483-508.

3. McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P.J., and Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. Philos. T. Roy. Soc. B. 363(1509), 3515-3528.

4. Mesoudi, A. (2011). An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. Evol. Hum. Behav. 32(5), 334-342.

5. Vale, G.L., Flynn, E. G., Lambeth, S.P., Schapiro, S.J., and Kendal, R.L. (2014). Public information use in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). J. Comp. Psychol. 128(2), 215.

6. van de Waal, E., Renevey, N., Favre, C.M., and Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc. Roy. Soc. Lond. B. 277(1691), 2105-2111.

7. Farine, D.R., Spencer, K.A., and Boogert, N.J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. Curr. Biol. 25(16), 2184-2188.

8. Garland, E.C., Goldizen, A.W., Rekdahl, M.L., Constantine, R., Garrigue, C., Hauser, N.D., Pool, M.M., Robbins, J., and Noad, M.J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Curr. Biol. 21(8), 687-691.

9. Grüter, C., Leadbeater, E., and Ratnieks, F.L. (2010). Social learning: the importance of copying others. Curr. Biol. 20(16), R683-R685.

10. Leadbeater, E. (2009). Social learning: what do *Drosophila* have to offer?. Curr. Biol. 19(9), R378-R380.

11. Whiten, A. (2017). A second inheritance system: the extension of biology through culture. The Royal Society, Interface Focus 7(5), 20160142.

12. Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340(6131), 485-488.

13. Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., and Boesch, C. (1999). Cultures in chimpanzees. Nature 399(6737), 682-685.

14. van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S., and Merrill, M. (2003). Orangutan cultures and the evolution of material culture. Science 299(5603), 102-105.

15. Claidière, N., Messer, E.J., Hoppitt, W., and Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. Curr. Biol. 23(13), 1251-1255.

16. Whiten, A., McGuigan, N., Marshall-Pescini, S., and Hopper, L.M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. Philos. T. Roy. Soc. B. 364(1528), 2417-2428.

17. Boyd, R., and Richerson, P.J. (1985). Culture and evolutionary process. (Chicago University Press).

18. Henrich, J., and Gil-White, F.J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol. Hum. Behav. 22(3), 165-196.

19. Rendell, L., Fogarty, L., Hoppitt, W.J., Morgan, T.J., Webster, M.M., and Laland, K.N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. Trends. Cogn. Sci. 15(2), 68-76.

20. Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. (2018). Social Learning Strategies: Bridge-Building between Fields. Trends. Cogn. Sci.

21. Baldini, R. (2012). Success-biased social learning: Cultural and evolutionary dynamics. Theor. Popul. Biol. 82(3), 222-228.

22. Horner, V., Proctor, D., Bonnie, K.E., Whiten, A., and de Waal, F.B. (2010). Prestige affects cultural learning in chimpanzees. Plos One 5(5), e10625.

23. Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., and Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. Evol. Hum. Behav. 36(1), 65-72.

24. Wrangham, R.W., Koops, K., Machanda, Z.P., Worthington, S. Bernard, A.B., Brazeau, N.F., Donovan, R., Rosen. J., Wilke, C., Otali, E., and Muller, M.N. (2016) Distribution of a chimpanzee social custom is explained by matrilineal relationship rather than conformity. Curr. Biol. 26(22), 3033-3037.

25. van de Waal, E., Bshary, R., and Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. Anim. Behav. 90, 41-45.

26. van de Waal, E., Borgeaud, C., and Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. Science 340(6131), 483-485.

27. Schuppli, C., Meulman, E.J.M., Forss, S.I.F., Aprilinayati, F., van Noordwijk, M.A., and van Schaik, C.P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. Anim. Behav. 119, 87-98.

28. Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. Anim. Behav. 136, 1-12.

29. Barrett, B.J., McElreath, R.L., and Perry, S.E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. Proc. Roy. Soc. B. 284, 20170358.

30. Cheney, D.L., Seyfarth R.M., and Smuts, B. (1986). Social Relationship and Social cognition in Nonhuman Primates. Sciences 234,1361-1366.

31. Henzi, P., and Lucas, J.W. (1980). Observations on the inter-troop movement of Adult Vervet Monkeys (*Cercopithecus aethiops*). Folia. Primatol. 33(3), 220-35.

32. van Noordwijk, M., and van Schaik, C. (1985). Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim. Behav. 33, 849–861.

33. Luncz, L.V., and Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. Am. J. Primatol. 76(7), 649-657.

34. Van Leeuwen, E. J., Acerbi, A., Kendal, R. L., Tennie, C., & Haun, D. (2016). A reappreciation of 'conformity'. Anim. Behav. 122, e5-e10.

35. Silk, J.B., Alberts, S.C., and Altmann, J. (2003). Social bonds of female baboons enhance infant survival. Science 302, 1231–1234.

36. Silk, J. B. (2007). Social components of fitness in primate groups. Science 317, 1347–1351.

37. Kappeler, P.M. (2008). Genetic and ecological determinants of primate social systems. Ecology of social evolution 225-243.

38. Dobson, F.S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav. 30*(4), 1183-1192.

39. van de Waal, E., van Schaik, C.P., and Whiten, A. (2017). Resilience of experimentally seeded dietary traditions in wild vervets: Evidence from group fissions. Am. J. Primatol. 79(10).

40. Lucas, A.J., Burdett, E.R.R., Burgess, V., Wood. L.A., McGuigan, N., Harris, P.L. and Whiten, A. (2017). The development of selective copying: children's learning from an expert versus their mother. Child. Dev. 88, 2026-2042.

41. Frick, A., Clément, F., and Gruber, T. (2017). Evidence for a sex effect during overimitation: boys copy irrelevant modelled actions more than girls across cultures. Roy. Soc. Open. Sci. 4(12), 170367.

42. Cross, C.P., Brown, G.R., Morgan, T.J., and Laland, K. N. (2017). Sex differences in confidence influence patterns of conformity. Brit. J. Psychol. 108(4), 655-667.

43. Burdett, E.E.R., Lucas, A.J., Buchsbaum, D., McGuigan, N., Wood, L.A., and Whiten, A. (2016). Do children copy an expert or a majority? Examining selective learning in instrumental and normative contexts. Plos One 11(10), e0164698.

44. Wood, L.A., Harrison, R.A., Lucas, A.J., McGuigan, N., Burdett, E.R.R., and Whiten, A. (2016). 'Model age-based' and 'copy when uncertain' biases in children's social learning of a novel task. J. Exp. Child. Psychol. 150, 272-84.

45. Whiten, A. (2017). Culture extends the scope of evolutionary biology in the great apes. Proc. Natl. Acad. Sci. USA 114, 7790-7797.

46. Mucina, L., and Rutherford, M.C. (2006). The vegetation of South Africa, Lesoto and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria. Memoirs of the Botanical Survey of South Africa.

47. Cheney, S.L. (1981). Intergroup encounters among free-ranging vervet monkeys. Folia primatologica 35(2-3), 124-146.

48. Cheney, S.L., and Seyfarth R.M. (1990). How monkeys see the world. Isbell & Pruetz Eds. (University of Chicago Press). 375 p S4.

49. Walters, J.R., and Seyfarth, R.M. (1987). Conflict and cooperation. In B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, T.T. Struhsaker Eds. Primate societies. (University of Chicago Press). 306–317p.

50. Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., and Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 82(4), 911-921.

51. Csillery, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B., Spong, G., and Pemberton, J.M. (2006). Performance of markerbased relatedness estimators in natural populations of outbred vertebrates. Genetics 173 (4), 2091-2101.

52. Schnider, A. (2016). Family first: The effect of relatedness on socio-positive behaviors in female vervet monkeys (*Chlorcebus aethiops pygerythrus*). MSc thesis, Department of Anthropology, University of Zurich, Switzerland.

53. Wang, J.L. (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Mol. Ecol. Resour. 11 (1), 141-145.

54. Milligan, B.G. (2003). Maximum likelihood estimation of relatedness. Genetics 163, 1153–1167.

55. Newman, T. K., Fairbanks, L. A., Pollack, D., Rogers, J. (2002). Effectiveness of human microsatellite loci for assessing paternity in a captive colony of vervets (Chlorocebus aethiops sabaeus). Am. J. Primatol. 56, 237-243.

FIGURE LEGENDS

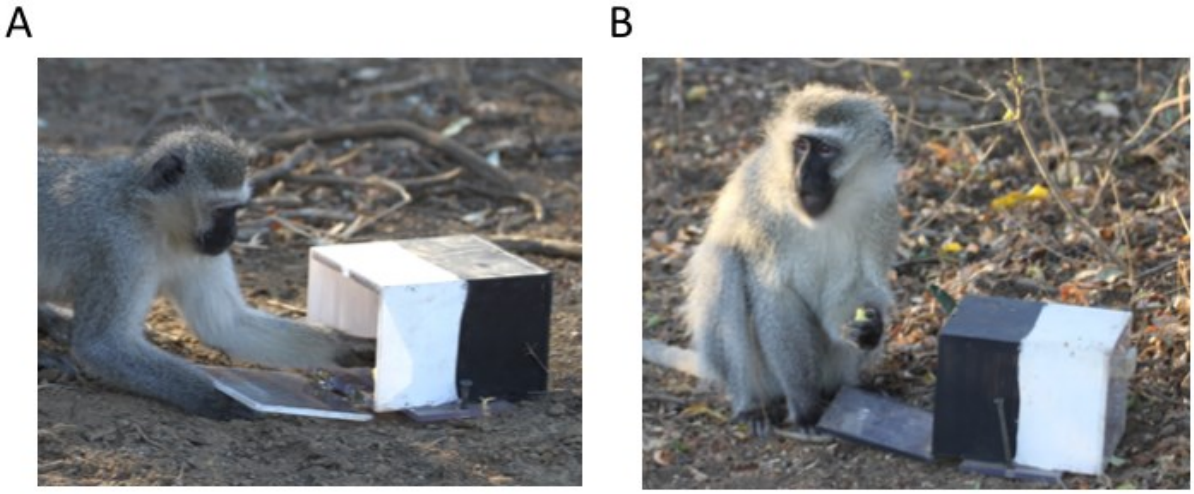
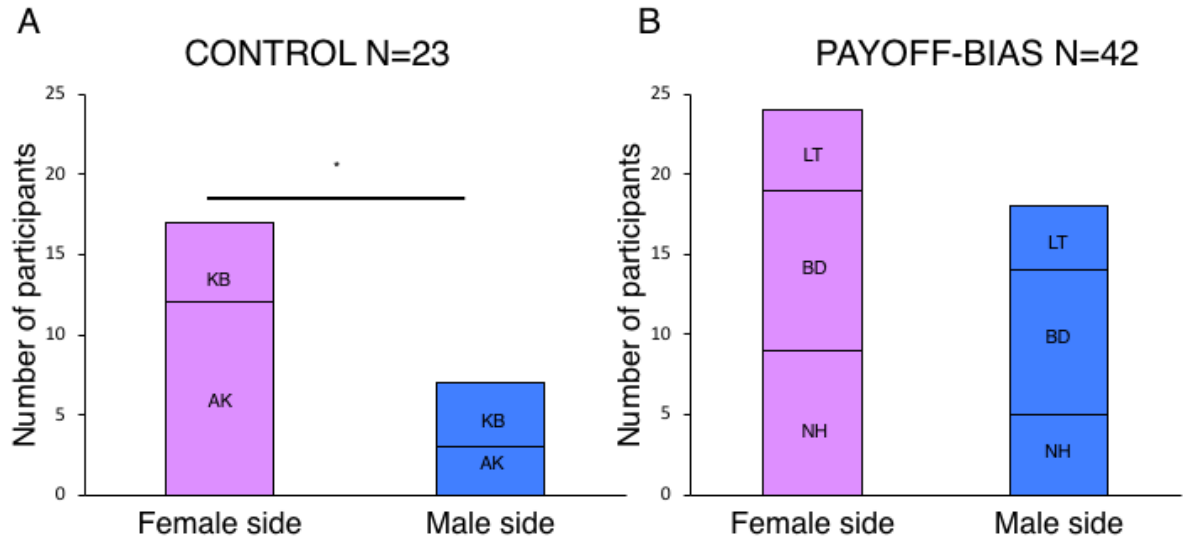
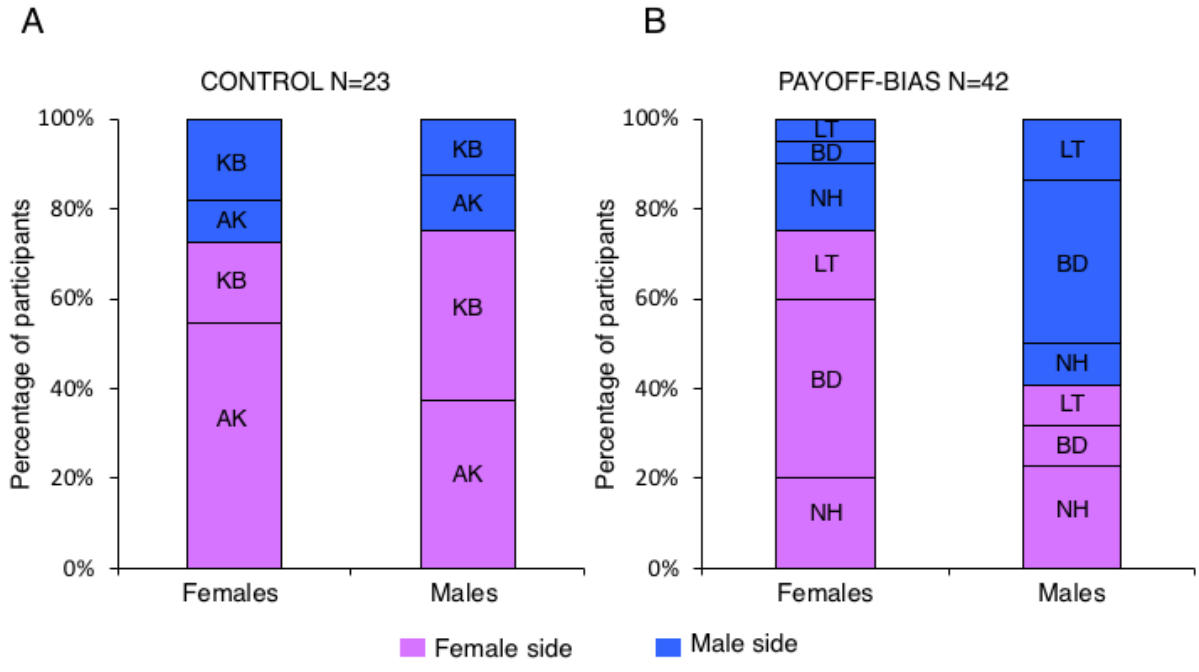


Figure 1. Experimental design. A) adult female opening on the white side of the box, B) adult male opening on black side of the box. Photographs copyright: Erica van de Waal. See also Table S1 and supplemental video S1, S2 and S3.



411

412 **Figure 2. First Manipulation.** Number of individuals who chose the female side or male side
413 as their first choice depending on the experimental condition: A) Control, B) Payoff-bias
414 favoring males. The letter codes (AK, KB, BD, LT, and NH) represent the name codes of the
415 different experimental groups, and the delimitations on each histogram represent the number
416 of participants in each group. See also Table S2, S3, and S4.



417

418

419 **Figure 3. Influence of the sex of participant on the first manipulation.** Proportion of side
420 chosen first, depending on the sex of the participant according to experimental condition: A)
421 Control, and B) Payoff-bias; The letter codes (AK, KB, BD, LT, and NH) represent the name
422 codes of the different experimental groups. AK and KB represent the two controls group, and
423 BD, NH and LT represent the three payoff-bias groups. See also Table S2, S3, S4 and S5.

424 **TABLES**

Dependent Variable= side chosen first	Fixed factors	Test value (Type III)	F value	ddl	P Value
Payoff-bias context	Sex	1.927	9.887	1	0.005**
	Age	0.175	0.897	1	0.354
	Rank	0.004	0.022	1	0.883
	Kinship male model	0.349	1.791	1	0.194
	Kinship female model	0.064	0.330	1	0.571
	Group	0.735	1.885	2	0.176
Control context	Sex	0.036	0.174	1	0.683
	Age	0.068	0.329	1	0.576
	Rank	0.069	0.333	1	0.573
	Kinship male model	0	.	.	.
	Kinship female model	0.124	0.599	1	0.452
	Group	0.067	0.326	1	0.577

Table 1. Testing multiple factors influence on first choice. Summary of results of the GLM Models with all dependent variables, fixed effects, and interactions. The first GLM model analyzed the effects of the sex, age, rank, group or kinship with male model and kinship with female model, of the participants on the first choice participants made in the context of payoff-bias. The second GLM model analyzed the effect of the sex, age, rank, group or kinship with male model and kinship with female model, of the participants on the first choice participants made in the control condition. Significant differences are indicated by ** p= 0,005. See also Table S5.

STAR ★METHODS

Detailed methods are provided in the online version of this paper and include the following:

KEY RESOURCES TABLE

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Erica van de Waal (erica.vandewaal@unil.ch).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All five studied groups (Ankhase, AK; Baie Dankie, BD; Kubu, KB; Lemon Tree, LT; Noha, NH), are part of IVP (Inkawu Vervet Project). They are wild monkeys, habituated to the presence of human since the start of the project in 2010. During the study, not counting infants, the group AK included 20 individuals (2 adult males, 4 adult females, and 14 sub adults and juveniles); the group BD included 43 individuals (4 adult males, 11 adult females, and 28 sub adults and juveniles); the group NH included 47 individuals (5 adult males, 13

449 adult females, and 29 sub adults and juveniles); the group LT included 30 individuals (4 adult
450 males, 9 adult females, and 17 sub adults and juveniles); and the group KB included 12
451 individuals (1 adult male, 6 adult females, and 5 sub adults and juveniles). Each individual
452 was identified using facial characteristics and natural ear-notches, or artificial ones made
453 during captures for genetic purposes. Monkeys were named with letter codes. Regularly
454 updated recognition files with portrait photographs and specific individual feature
455 descriptions were constructed for each group.

456 Ethics guidelines: We adhered to the "Guidelines for the Use of Animals in Research" of the
457 Association for Study of Animal Behaviour. Our experiments were approved by the relevant
458 local authority, Ezemvelo KZN Wildlife, South Africa; and by the funders. The setup of this
459 experiment could involve opportunities for competition over food. However, we offered
460 either several boxes at the same time or a single box for isolated individuals in order to
461 minimize conflicts. We also kept the amount of food provided in every session relatively
462 small during both phases of this experiment.

463 METHOD DETAILS

464 Study site

465 Experiments were conducted at the Inkwavu Vervet Project (IVP) between 17th of February
466 2016 and 21st of July 2017 on five groups of wild vervet monkeys (*Chlorocebus pygerythrus*).
467 IVP is located in « Mawana », a private game reserve of 10,000-hectares, in KwaZulu Natal,
468 South Africa (S 28°00.327 ; E 31°12.348). The reserve is mainly used as a hunting farm but a
469 portion of the land is reserved for the study of vervet monkeys. The vegetation is classified as
470 Savannah biome characterized by areas of grasslands with dispersed singular or clusters of
471 trees, with the typical savannah thornveld, bushveld and thicket patches [46]. The reserve is
472 inhabited by all the usual savannah mammals, except for black rhinoceroses, buffaloes,

473 cheetahs and lions. Therefore, vervet monkeys can face their main potential predators:
474 leopards, hyenas, jackals, pythons, cobras, mambas, puff adders, baboons, and different
475 raptors [47].

476 Hierarchy

477 Females were considered adult when they gave birth for the first time; males after their first
478 dispersal. Females are philopatric. Males disperse several times throughout their lifetime.
479 They occupy the lowest rank when they first arrive in a new group but this can change
480 depending on the relationship they establish with the females. Otherwise vervets exhibit a
481 linear dominance hierarchy [48, 49]. Rank in females is inherited, with the youngest female
482 offspring acquiring the rank directly below that of her mother and the older female offspring
483 following in rank. Whilst the male hierarchy changes depending on migrations, strength and
484 acceptance by females, the female hierarchy is relatively stable [39], including in this
485 population [28]. Males and females have separate hierarchies [48]. In order to identify the
486 rank of each individual, hierarchy analyses were run [50] using the R package 'EloRating'
487 [51] for adult males and females separately, with conflict data collected ad libitum from the
488 groups.

489 Kinship

490 In order to assess the kinship between individuals, we calculated the degree of relatedness.
491 Tissue samples were obtained when individuals were trapped and anaesthetized in order to be
492 provided with a radio collar, while fecal samples were collected on a regular basis since the
493 beginning of 2013 during weekly follows. When an identified individual defecated, parts of
494 the feces were collected and stored according to the established sampling protocol
495 (http://www.aim.uzh.ch/de/research/orangutannetwork/gsp.html). Samples were dried and

496 stored in the field station in South Africa, before being sent to the University of Zurich,
497 Switzerland, for analyses.

498 We extracted DNA using Quiagen's DNeasy and QIAmp Stool Mini kit following the
499 manufacturer's protocol, with the following modifications. For each sample, 85mg to 180mg
500 of feces were weighed and mixed with 1.7µl of Buffer ASL and 5 µl of Proteinase K and
501 subsequently incubated in the overhead rotator overnight at 55°C. An additional 1.5µl
502 Proteinase K was added to both fecal and tissue samples after one night of incubation,
503 followed by overhead rotation for an additional hour. For fecal samples, the centrifugation
504 time after addition of the InhibitEx tablet was increased to 8 min in order to stabilize the
505 pellet. Fecal samples were further processed with the QIacube robotic workstation (Qiagen)
506 and the concentration of all samples was measured with the NanodropR-100 (Software 3.3).

507 In order to estimate kinship between individuals, we calculated dyadic relatedness (r) using
508 17 autosomal microsatellite loci [52]. As the choice of the most accurate estimator depends on
509 inherent population structure and history [53], we used the program Coancestry 1.0.1.5 to
510 determine the best performing relatedness estimator (*i.e.*, high precision and low standard
511 deviation). We included all adult individuals plus all juveniles who took part in the
512 experimental procedure, totaling 172 individuals. For seven different relatedness estimators,
513 we simulated 1,000 pairwise relatedness values (r-values) for unrelated dyads (expected r =
514 0), half-siblings (r = 0.25), full-siblings (r = 0.50), and parent-offspring (r = 0.50), using
515 allele frequencies obtained from all 172 genotyped individuals. Based on this analysis, we
516 found dyadic likelihood estimator MEst [54] to be the best performing.

517

518 Data collection

519 The field experiment was conducted by AB, alone or with the help of one or two other staff
520 members of the Inkaw Vervet Project (IVP). Prior to the experiment, each staff member had
521 to pass an identification test, assessing their ability individually recognize all monkeys of the
522 studied group. All observers also had to pass an inter-observer reliability tests to ensure high
523 consistency in data collection. Experiments were mainly conducted in winter because natural
524 food resources being less abundant at this time of the year, monkeys were more motivated to
525 participate. Experiments took place in five different groups, three groups with the payoff bias
526 in place (Baie Dankie group, Noha group and Lemon tree group) and two control groups
527 (Ankhase group and Kubu group).
528
529 Training
530 We first trained our models, the dominant male and the dominant female of each group, to
531 open their side of the box, either black or white side. The colors were counterbalanced across
532 the different experimental and control groups. When the alpha female or male was too shy to
533 participate and get trained, we trained the next-highest ranking individual. In group KB the
534 second female in the hierarchy was the model (daughter of the alpha female). In group LT, the
535 model was the female of the second matriline of the group (as the females from the alpha
536 family were too shy to approach the experimental setup, even during the experimental phase,
537 perhaps because this group is less habituated to humans than the other groups); this female
538 was still high ranking and had the 4th position in the hierarchy order (out of 9 adult females in
539 total). In NH, the second female was the model; she was the sister of the alpha female. For all
540 the other groups, male and female models were the alpha individuals.
541 The food reward given inside the box was one piece of an apple that all monkeys were
542 already used to eating in other experimental settings. One apple was cut into 20 pieces, so one
543 piece at the time was given to the monkeys, and in payoff-bias condition only male models

544 got five pieces of apple instead of one. We always used apples of the same size in each
545 particular session, to have regular sized pieces, and in each session, both models were trained.
546 Except for the alpha male in the group KB, for who we had to use pieces of corn as a reward,
547 in order to motivate his participation in the experiment, because he was not willing to
548 participate with apples. The reward for both models in this group and for participants to the
549 experiment was five pieces of corn.

550 During the demonstration, we recorded the attentional state of group members around the
551 box. An individual was considered as attending if it was inactive and had its head and body
552 oriented towards the model opening the box in a 10m radius of the demonstration.

553

554 Experimental phase

555 The experimental phase started when a minimum of two-thirds of the group had seen both
556 models opening the box. Following this rule, we fixed the numbers of opening for each model
557 to 100 times. During both the demonstration and experimental phases, once the box was
558 opened and empty, an experimenter rebaited it.
559 During the experimental phase, we offered the same box. Monkeys had access to one piece of
560 apple placed in the middle of the box (five pieces of corn for KB group to stay consistent);
561 this in payoff-bias and control contexts, so the reward in the box could be monopolized by the
562 monkey opening the box. All monkeys were free to interact and free to try to open the box
563 within the constraints of the social group dynamics, such as rank. Also, in order to have as
564 many individuals as possible trying to manipulate the box at least once, we offered the box in
565 different ways. First, six boxes were offered early in the morning at the sleeping site, before
566 the group started moving. But this method led to mostly high-ranking individuals accessing
567 the boxes and monopolizing them. So, we also offered a single box to isolated individuals
568 when the group was moving, in order to provide them with the opportunity to manipulate the

box. For each manipulation of the box during the experimental phase, we recorded in the field the identity of the monkey manipulating the box, the side chosen, whether or not it managed to open the box and obtain the reward, which group members were attending the opening, and the identity of all group members within a 5 and 10 m radius of the box. All interactions with boxes were recorded using a video camera. For both phases we could perform one session per day, and a session was ended when an individual ate a total of: one apple for an adult female, two apples for an adult male, or 25g and 50g of corn for female and male, respectively.

The demonstration phase and experimental phases were done opportunistically across multiple days. The average duration of the demonstration phase was of 55 minutes, and the experimental phase session was of 70 minutes.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed in SPSS (24.0). We conducted proportion tests in order to see if individuals choose one side preferentially during their first choice, across the three experimental phases. We calculated Spearman correlation coefficients to test for a correlation between the first choice made by participants and their attentional state (*i.e* the amount of time individuals watched each model opening its side of the box during the demonstration phase and the amount of time they saw other individuals attempting to open either side of the box during experimental phase). We also tested whether group members were attending more or not to one model or the other using a Wilcoxon paired test (see supplemental information). Then, we used Generalized Linear Models (Table 1, see also table S5 in supplemental information) to control for potential effects of factors including sex, rank, kinship with male model, kinship with female model, age and group identity, on the first choice made by participants. We ran this GLM (Type III) for both the payoff-bias condition and the control condition. Side chosen first was included as the dependent variable, while sex,

age, kinship, rank, and group of belonging, were all considered as fixed factors. We first ran the GLM including all interactions possible between all the factors, but since no results were significant concerning these interactions, we ran the final GLM testing only the effect of the different factors in order to retain statistical power. Finally, we conducted proportion tests in order to compare separately males and females on the effect of the experimental setup (control or payoff) on their first choice.

We had to remove one individual from our analyses (Pue) as he managed to open the box during the demonstration phase. Also, in the analyses we did not take into account two males from BD (Hwa and Ubu), because they integrated into the group after the demonstration phase. Individuals younger than one year old did not participate in the experiment.

The analyses concerning the attention of group members during the demonstration phase, revealed that there is no correlation between the first choice made by participants in both conditions and 1) the number of participants they watched opening the box (model included), 2) the last side they saw being opened by a model, and 3) the last side they saw being opened by the model or another participant, (see Table S2).

Also, our data showed no significant difference in the attention of group members towards male models or females models (Wilcoxon paired test: payoff-bias condition: $Z= -1.642$; $p=0.101$; $n=42$; control condition: $Z= -0.852$; $p=0.394$; $n=23$), contradicting previous results where selective attention was found only towards the female model when the experimental setup involved only one model per group [6]. It is possible that in our specific experimental set up, individuals became interested in the boxes, perhaps by having the dominant female involved, and then paid attention to openings by both models.

Furthermore, we controlled the females' first choice in both experimental contexts (payoff-bias and control) using a Fisher exact test (due to the small sample size) ($Chi2= 0.019$; $df= 1$;

618 p=0.890; N=31) and we found that females did not copy the female side in the payoff-bias
619 context significantly more than the control.

620 Finally, to support the results found with the GLM as illustrated in Figure 2 and Figure 3, we
621 also conducted another statistical test to confirm that the group of belonging had no influence
622 on the first choice made by participants. Indeed, with this test we also did not find any effect
623 of group of belonging (control condition: Mann-Whitney U test: U = 49.5, N= 23, p=0.506;
624 payoff-bias condition: Kruskal-wallis test: Chi2= 1.115, N=42, p=0.573). Running the GLMs
625 including group as random factor provided essentially the same results as in the other GLMs,
626 see table S5.

627 **SUPPLEMENTAL INFORMATION**

628 **Video S1. Adult male model opening the black side of the box during the demonstration**
629 **phase and getting five pieces of apple. Related to Figure 1 and Table S1.**

630 **Video S2. Adult female model opening the white side of the box during the**
631 **demonstration phase and getting one piece of apple. Related to Figure 1 and Table S1.**

632 **Video S3. Sub-adult male opening the box during the experimental phase. Related to**
633 **Figure 1 and Table S1.**

634